

Observations and Experiments on the Food Habits of California Sea Hares of the Genus *Aplysia*

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IN A PREVIOUS PAPER the senior author (Winkler, 1959a) presented the results of fecal pellet analyses to determine the influence of diet on the color of *Aplysia californica* Cooper. Only the dominant plants were mentioned in connection with that immediate problem. The present paper contains more detailed information from that study and from subsequent observations and reviews of references to *Aplysia* food plants.

The food of *A. californica* has received only limited consideration in connection with other studies. This is also true, however, of *Aplysia* species in general. Even in the large monograph of Mazzarelli (1893) the only indication of the nature of the food is in a discussion of the method of feeding, where we find the phrase "... algae (ordinarily *Ulva lactuca*) which serves as nutriment." In the extensive study of European *Aplysia punctata* by Eales (1921), about half a page is concerned with food. She notes an apparent change in food habits with age. The young, she says, live on red seaweed like *Delesseria* [probably *D. sanguinea*] and then slowly migrate through the *Laminaria* zone, where they feed on *Laminaria*, into shallow water, where the fully grown adults live on *Fucus* and *Ulva*. However, since she also states that they are found in the greatest numbers in the *Zostera* beds, it may be that like *Aplysia californica* they also feed on *Zostera*.

As to the feeding habits of *A. californica*, MacGinitie (1935) stated that the animal eats *Zostera* in Elkhorn Slough. In a later work (MacGinitie, 1949) he stated that they eat "seaweeds." Winkler (1959a) referred to three red

seaweeds used as food by *Aplysia californica* and to their effect on the color pattern. Another paper (Winkler, 1959b) mentions the effect of diet, both qualitatively and quantitatively, on the purple secretion. Winkler (1961) mentions diet in connection with two special habitats which are reported here in more detail. Marcus (1961) stated that *A. californica* eats seaweeds, "especially *Zostera* and *Codium*."

MATERIALS AND METHODS

Young specimens of *Aplysia californica* 4-5 inches long were captured on the central shore area of Lunada Bay, Palos Verdes, California, and each was placed in an individual pint fruit jar until fecal pellets were passed. The pellets were then removed to small screw-capped vials and the animal was released at sufficient distance to preclude resampling. Twenty-five specimens from this area were sampled in this manner. Pellets were also collected from larger specimens wandering in the deeper waters of the bay and from 1 mile north of the north side of Palos Verdes Point. The pellets were kept under refrigeration until examined and identified by the junior author. Since the efficiency of sea hare digestion appears to be in indirect proportion to the rate and quantity of food ingestion, identification of the algae offered no great problem since these sea hares were well fed.

Observations on specimens taken from Doheny Beach, California, and from a small lagoon at Lunada Bay, possessing a different flora than the former, are also reported. The food plants determined from crop contents were made during other studies involving the sacrifice of the animals.

RESULTS

Results from 25 young specimens taken from Lunada Bay in 1955 are presented in Table 1. In this area the following seaweeds were noted

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TABLE 1
DIET OF YOUNG *Aplysia californica* AT LUNADA BAY

KINDS OF PLANTS*	NO. SPECIMENS IN WHICH FOUND	NO. SPECIMENS IN WHICH DOMINANT
<i>Acrosorium uncinatum</i>	1	1
<i>Centroceras clavulatum</i>	8	4
<i>Ceramium eatonianum</i>	21	14
<i>Corallina vancouveriensis</i>	12	1
<i>Gelidium coulteri</i>	11	2
<i>G. crinale</i> (?)	7	1
<i>Gelidium</i> sp.	1	0
<i>Gigartina canaliculata</i>	14	7
<i>Hypnea valentiae</i>	4	2
<i>Lophosiphonia</i> sp.	1	0
<i>Phyllospadix</i> sp.	6	0
<i>Plocamium pacificum</i>	12	2
<i>Pterocladia</i> sp.	4	0
<i>Pterosiphonia</i> sp.	2	0
<i>Spermothamnion snyderae</i>	1	0
<i>Sphacelaria</i> sp.	2	0
<i>Ulva</i> sp.	2	0

* Although marked differences in the relative abundances of the various algae in the habitat would seem to negate the validity of this table in indicating selectivity of food by the sea hares, there is some interesting supporting evidence. Although *Gigartina canaliculata* was the dominant intertidal rock-cover alga throughout the area, and was eaten, it appeared far less dominant in the pellets than the small, relatively inconspicuous epiphytic alga *Ceramium*. Similarly, although *Ulva* and *Plocamium* were so sparse in the areas as generally to go unnoticed, these, especially the latter, appeared in the pellets.

to be common, though never found in the fecal pellets: *Laurencia splendens*, *Chondria californica*, *Gigartina leptorhynchus*, *Prionitis lanceolata*, *Laurencia subopposita*, *Cystoseira osmundacea*, *Gymnogongrus leptophyllus*, *Bossea orbigniana*, *Herposiphonia* sp., *Rhodymenia* sp., and *Colpomenia sinuosa*.

All specimens taken from deeper water in Lunada Bay and off Palos Verdes Point were similar in the algal content of their pellets. In every case the dominant plant was *Plocamium pacificum*, but with some admixture. These admixtures included *Phyllospadix* sp., *Lophosiphonia* sp., *Gelidium* (several species), and *Ceramium eatonianum*.

In May 1961 the larger red-striped *A. californica* from Lunada Bay were found feeding exclusively on the red alga *Laurencia pacifica*, which turned their blood and digestive glands a deep red.

Observations of the crop contents of several hundred *Aplysia* specimens were made during the course of work in 1959 at the Lunada Bay lagoon. Occasional spot checks were made in which the contents were determined as to species, but no single alga was recognized as dominant. The samples contained: *Chondria californica*, *Lithothrix aspergillum*, *Ceramium eatonianum*, *Centroceras clavulatum*, *Plocamium pacificum*, *Corallina gracillius*, and *Ectocarpus* sp., intermixed with fragments of coralline algae. The flora of this small lagoon contained more coralline algae and much less *Gigartina canaliculata* than the afore-mentioned 1955 collection site located 1/4 mile to the south on Lunada Bay.

The collecting area at Doheny Beach was located at the extreme north end of the state park, where a small lagoon of uniformly shallow water is protected on the north by a stratified rocky peninsula submerged at higher tides, and on the south by a wave-formed reef of small boulders and gravel. The flora was comparatively limited, consisting predominately of various jointed coralline algae with intertwined *Hypnea valentiae*. Algal growth improved as one moved to the seaweed area of the lagoon. In this habitat 86 specimens were collected, but because of apparently grossly similar crop contents only 8 specimens were analyzed for presentation in Table 2. Collection dates were March 24, 1959, for numbers D-02 to D-08, and April 29, 1959, for the remainder. It will be noted that the latter collection shows a greater specialization of diet than the former and may reflect the concentration of sea hares farther out in the lagoon than at the former collection date. It may, on the other hand, suggest that the sea hare tends to become more selective in its food as it becomes older. This has generally been noted from other areas.

The algal contents of crops of *Aplysia vacaria* have also been examined. Animals collected in their usual haunts in the *Egregia* beds have contained only large amounts of *Egregia* in their crops. On the other hand, when the animals are inshore in breeding aggregations the crops are usually empty or contain sand or other material of little significance. On one occasion only, several such animals were found

to have ingested a quantity of *Pelvetia fastigiata*, a food plant that was consistently refused by aquarium-confined specimens (Winkler, 1955). The diet of the young of this species has not been determined.

DISCUSSION AND CONCLUSIONS

In northern California *Aplysia californica* is known principally from protected bays and estuaries such as Elkhorn Slough, Bodega Bay, and Tomales Bay. In these areas, beds of *Ulva* and *Enteromorpha* often occur abundantly, and J. J. Gonor has reported to us in a personal communication that *A. californica* lives in these beds and apparently uses both plants for food. Marcus (1961), reporting upon specimens from Bodega Bay and Tomales Bay, indicated that *A. californica* feeds on sea plants, especially *Zostera* and *Codium*. MacGinitie (1935) stated that sea hares in Elkhorn Slough fed on *Zostera*, but in subsequent personal correspondence has indicated that they also fed on *Enteromorpha*, which is sometimes the most prevalent plant in the slough. However, he also observed that at certain seasons the alga was absent from the area while *Zostera* remained. He concluded, then, that *Zostera* was their principal staple food.

In southern California the eel grass, *Zostera*, does not occur intertidally on the open coast and is uncommon in bays, and although the

similar surf grass, *Phyllospadix*, grows in profusion at low water levels it is rarely ingested by sea hares. Likewise, neither *Ulva* nor *Enteromorpha* is abundant in open coast habitats of southern California, and, although captive sea hares showed preference to *Ulva* or *Enteromorpha* over any other food offered them in the laboratory, in nature they resort to feeding on red algae, which are almost their exclusive food.

Young southern California sea hares seem to eat a wide variety of seaweeds depending upon the flora in their immediate surroundings, although some species are apparently habitually refused. As they grow older and wander farther they seem to become more selective in their food habits and develop a behavior pattern that is difficult to break under changed feeding conditions in the laboratory.

It has been generally observed that *Aplysia californica* in northern California is of larger average size than in southern California, and the senior author considers that this larger size, as well as the difference in color (Winkler 1959a), results from dietary differences. Experimental evidence for the variation in size similar to that for color variation is needed to confirm the homogeneity of the two forms. Two distinctive dietary factors offer themselves for study: (1) the comparative nutritive value of a high *Ulva-Enteromorpha* component in the diet during spring and summer; (2) the effect of almost exclusive feeding on the marine grass,

TABLE 2
PRESENCE AND RELATIVE ABUNDANCE OF SEVERAL ALGAE IN CROPS
OF *Aplysia californica* FROM DOHENY BEACH, CALIFORNIA

COLLECTION NO.	<i>Hypnea valentiae</i>	<i>Jania tenella</i>	<i>Corallina gracilis</i>	<i>Corallina pinnatifolia</i>	<i>Corallina vancouveriensis</i>	<i>Sphacelaria</i> sp.	<i>Laurencia</i> sp.	<i>Lithothrix aspergillum</i>
D-02	XXX	X						
D-04	XX		XX					
D-06	X	XXX						
D-08	X	X	X	X		X	X	X
D-20	XXXX							
D-21	XXXX							
D-27	XXXX							
D-28	XXX				X			

Zostera marina, during winter. Further studies are also needed on the diet of adult *Aplysia californica* which, according to Limbaugh (personal communication) are most numerous at depths of 30–40 ft and have been observed as deep as 100 ft, depending upon concentrations of plants. He mentions them eating the "thinner red and green seaweeds."

From evidence now available it would appear that *Aplysia californica* and *A. vaccaria* are not competitive for food, and that the former uses red and green algae as well as marine phanerogams for food, while the diet of the latter is essentially restricted to the brown alga *Egrecia*, at least in the tidal zone. The nutritive value of *Egrecia* seems to favor growth to large size, for Limbaugh has reported observations of specimens of *A. vaccaria* in the subtidal zone measuring up to 30 inches and an estimated 35 lb, making them the giants of the gastropoda.

SUMMARY

Young *Aplysia californica* on the open coast of southern California subsist on a diet mainly of fleshy red algae but show a preference for *Ulva* or *Enteromorpha* under artificial feeding. In the northern end of its range, where it appears to become largely estuarine in habitat, all reports indicate that it feeds almost exclusively on green algae and eel grass, *Zostera marina*. It is suggested that the dietary differences may influence its size as well as its color, and that an adequate winter food supply is an important factor.

A. vaccaria appears to feed exclusively on the brown alga, *Egrecia*.

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